

Intensity of melanin-based color and risk of predation in the Barn Swallow *Hirundo rustica*

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Abstract. Predators are supposed to exert strong selection pressures on their prey, especially when phenotypic traits such as secondary sexual characters promote mating success at the expense of costs in terms of natural selection. Signaling theory predicts that individuals of superior phenotypic quality will enjoy an advantage in term of mating success, but also in term of natural selection, if such individuals are in prime condition both before and after development of exaggerated secondary sexual characters. We tested this prediction in the Barn Swallow *Hirundo rustica* being preyed upon by the Eurasian Sparrowhawk *Accipiter nisus*, using extensive samples of feathers from prey and non-prey. We measured tail length and coloration of outermost tail feathers in the black area of the proximal and distal part of tail feathers, but also the white spot of the tail feathers. Prey had significantly less dark distal, but not proximal parts of their tails, while there was no difference in coloration of the white spot between prey and non-prey. Prey had significantly paler tail feathers than non-prey, especially among long-tailed individuals. These results suggest that Barn Swallows with long tails that fail to deposit large amounts of melanin in their tail feathers run an elevated risk of predation.

Key words: coloration, ornaments, predation, sexual selection, signals, Sparrowhawk

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INTRODUCTION

The evolution of ornamental traits has been a major issue of research in animal communication during the last three decades. Although the intensity of sexual selection acting on such characters is ultimately limited by natural selection, the interaction between these two evolutionary processes is not well understood. Arguments from signal theory (Zahavi 1975, 1977, Hasson 1997) state that for honest signals to evolve, it is necessary that production and maintenance costs are imposed on signalers, and that such costs are higher for individuals of low genotypic or phenotypic quality. While several mechanisms have been proposed for production costs of signals (e.g., Espmark et al. 2000, Møller et al. 2000, Galván & Alonso-Alvarez 2008), maintenance costs, which reflect the intensity of natural selection, have received much less attention (Bortolotti 2006). Predation risk is proba-

bly the most evident maintenance cost for elaborate sexual signals, although the role of predation in the evolution of these traits has only rarely been considered (but see Endler 1980, Møller 1989, Petrie 1992, Götmark 1993, Götmark & Unger 1994, Møller & Nielsen 1997).

The level of sexual signaling is positively related to survival prospects, either linearly (e.g., Alatalo et al. 1991, Møller 1991, Borgia 1993, Saino et al. 1997, Galván & Møller 2013) or through a quadratic relationship (Figuerola & Senar 2007), indicating that only high quality individuals are capable of bearing the handicap imposed by costly signals. Only few studies have directly related risk of predation to the level of exaggeration of such signals, and these few studies show that low quality individuals (i.e. those with less exaggerated traits) pay higher costs in terms of predation risk (Endler 1980, Petrie 1992, Møller & Nielsen 1997; but see Møller 1989). Thus, only fit individu-

als can produce highly elaborate traits. This claim is supported by the observation that differential predation is linked to measures of immunity that potentially mediate the cost of secondary sexual characters (e.g., Møller & Erritzøe 2000).

The classical sexual selection theory predicts that conspicuous individuals or species pay a cost in terms of predation risk because they are more easily detected by predators (Götmark 1993, Slagsvold et al. 1995, Dale & Slagsvold 1996, Rytkönen et al. 1998, Møller & Nielsen 2006). From a camouflage perspective, this phenomenon is also responsible for the maintenance of certain color polymorphisms (Stuart-Fox et al. 2003, Horth 2004 and references therein). At the intraspecific level, the most conspicuous individuals are supposedly those in prime condition (Hill & McGraw 2006, Penteriani et al. 2008). Such individuals can more readily cope with the costs of elaborate traits without compromising survival, and they should thus be able to avoid predators more easily than low quality individuals (the unprofitable prey hypothesis; Götmark 1992, 1993, 1995, Caro 1995). Although some authors have found relationships between the probability of survival and the coloration of animals, as far as we know all these studies are based on the (reasonable) assumption that the disappearance of individuals was due to predation (e.g. Cain & Sheppard 1954, Kettlewell 1973, Endler 1980, Figuerola & Senar 2007), but currently there is only one report of direct predation events, and this corresponds to a mammal species (Penteriani et al. 2008).

The Barn Swallow *Hirundo rustica* is a monogamous, aerially-feeding insectivorous passerine with the outermost tail feathers acting as a secondary sexual trait used in female choice. Males with longer and more symmetrical tails obtain higher mating success and have higher viability (Møller 1994, Saino et al. 1997). Møller & Nielsen (1997) showed that Barn Swallows that fell prey to Eurasian Sparrowhawks *Accipiter nisus* had shorter and more asymmetrical tails than birds that survived the breeding season, indicating that natural selection acts against individuals with traits that reflect low quality. This is expected from an honest signaling hypothesis because high quality individuals should be able to overcome the costs of extravagant ornaments without compromising their viability. That should not be possible if they did not also have a higher ability to avoid predators than individuals with the smallest ornaments.

The aim of the present study was to quantify differential predation by Sparrowhawks on Barn Swallows with respect to tail coloration, and determine whether such predation depends on individual quality by using tail length as an indirect indicator of quality. Except for a white spot located at the middle of tail feathers, the tail of Barn Swallows is non-iridescent black and melanin-based, as deduced from the shape of its reflectance curve (see Fig. 1a; McGraw 2006). Results from biochemical analyses indicate that the melanin content of these feathers is mostly composed of eumelanin, and no other pigments such as carotenoids have been found (J. J. Negro, pers. comm.). Melanin has an important role in feathers by increasing, among other properties, their stiffness and resistance to abrasion (McGraw 2006, Schreiber et al. 2006). Given that the outermost tail feathers provide aerodynamic benefits to Barn Swallows (Norberg 1994), and that mechanical fatigue decreases the stiffness of feathers (Borgudd 2003), strengthening the tail through melanin deposition should be of major importance in this species that performs long-distance migrations and depends entirely on aerial insects for food. Because melanin content is reflected by the color of feathers (McGraw et al. 2005, Galván et al. 2012), and melanin can be physiologically costly to produce or environmentally constrained (Anderson et al. 2002, Poston et al. 2005, Fargallo et al. 2007, Galván & Alonso-Alvarez 2008, 2009, Galván et al. 2010, Hórak et al. 2010), a predation cost could be predicted for melanin-based coloration. Thus, paler or lesser conspicuous individuals (i.e. those with lower melanin content; McGraw et al. 2005) should be easier to capture by predators if melanin-based color is an indicator of stiffness of tail feathers and hence of individual quality. Because mainly high quality individuals should be able to overcome the costs imposed by long and presumably dark tails (see above), we predicted a relationship between tail length and coloration such that birds falling prey to Sparrowhawks should be those unable to produce tails of a length proportional to the amount of melanin in the tail feathers. A similar prediction was made for the color of the white spot of the tail, as previous studies have shown that the degree of whiteness is positively related to individual quality in other species (Hanssen et al. 2006, McGlothlin et al. 2007). Indeed, the size of this patch acts as a quality-revealing signal in Barn Swallows as shown by two different field experiments (Kose & Møller 1999, Kose et al. 1999).

Therefore, we predicted that birds falling prey to Sparrowhawks should have lower reflectance at the white spot of their tails than survivors.

MATERIALS AND METHODS

Study areas and samples of feathers

We obtained tail feathers from adult Barn Swallow prey of the Sparrowhawk collected in the field in a 250 km² study area in Vendsyssel, Denmark, in 1993 and 1994 by JTN, who recorded all prey items from the vicinity of 86 Sparrowhawk nests visited regularly during the breeding season of May and June. Details about how this was done have already been reported in detail elsewhere (Møller & Nielsen 1997). Tail feathers did not show signs of damage or degradation. All feathers were kept in plastic bags in complete darkness with the exception of brief periods used for color and morphological measurements.

We compared the tail feathers of prey with those of live adult Barn Swallows captured at breeding colonies at Kraghede (57°12'N, 10°00'E), less than 10 km from Vendsyssel, between May and June, with a few birds captured during July–September in 1989 and 1993–1994, using mist nets. The time of collection of prey feathers and the time of capture of live Barn Swallows was completely overlapping hence not posing a risk of bias. Live Barn Swallows may subsequently at a later stage fall prey to Sparrowhawks or other predators although that will not affect the analyses presented here because we used the standard procedure to demonstrate natural selection by comparison of two groups of individuals that were either dead or alive and that were retrieved simultaneously. The two outermost tail feathers were collected upon capture from a random sample of adults, placed in plastic bags, subsequently in an envelope and then in complete darkness until measurements were made.

Morphological measurements

We measured the length of the outermost tail feathers to the nearest mm using a ruler on the stretched feather. These measurements were highly repeatable when measured by an independent measurer (Møller & Nielsen 1997). The area of the white spot of tail feathers was calculated by using the equation in Kose et al. (1999). Individuals were sexed based on the presence of a brood patch (females). All others were considered to be males. Preys were sexed based on tail length and the size

of white spots on the tail feathers (see Kose & Møller 1999, Kose et al. 1999).

Color measurements

Plumage color was measured in the laboratory using an Ocean Optics USB2000 spectrophotometer (range 250–800 nm) with ultraviolet (deuterium) and visible (tungsten-halogen) lamps and a bifurcated 400 micrometer fiber-optic probe (Dunedin, Florida, USA). The fiber optic probe both provided illumination and obtained light reflected from the sample, and it had a reading area of ~1 mm². As previous analyses showed that the intensity of the color of Barn Swallow tails differs between distal and proximal parts of feathers (considering the white spot as a separation point; own unpublished data), and the basal part of the outermost feathers are covered by adjacent tail feathers when the tail is folded, color measurements were recorded separately for these three parts. Color of the proximal and distal parts could not be compared here, however, because the distal part of feathers is so thin that it was necessary to include the rachis, which is generally paler than adjacent feather barbs, producing changes in darkness along the feather due to the measuring area of the probe (only feather barbs were considered for measures taken on the proximal part and the white spot). The outermost tail feathers were placed on a black cardboard, and measurements were taken at a 90° angle to the sample. All measurements were relative to a white "Spectralon" tablet (WS-1-SS, Ocean Optics, Dunedin, Florida, USA), and reference measurements were frequently made to ensure that color measurements were made relative to the reference. For each feather, an average spectrum was obtained for three readings made on each feather part, each of them separated by the same distance. For some of the swallows that fell prey to Sparrowhawks it was possible to collect both outermost tail feathers, whereas only one was obtained from the others. Thus, mean values obtained from both feathers were considered when available. The same was done for the white spot but, due to the small size of this patch, measurements were taken from the same point removing the probe after each measure. Reflectance curves were determined by calculating the median of the percent reflectance in 10 nm intervals beginning at 300 nm and ending at 700 nm to cover the full spectral range that can be detected by birds (Cuthill et al. 2000). All measurements of coloration were done blindly with respect to origin of samples.

Mean reflectance spectra obtained for prey and survivors are shown in Fig. 1. Except for a slight increase in reflectance in the ultraviolet (UV) range, the spectral shape of proximal and distal feather parts is typical of a melanin-based color, with reflectance steadily increasing along the spectral range (McGraw 2006). The white spots presented a clear peak in the UV range (Fig. 1b).

Spectral data were summarized as a measure of total brightness, as this is the best predictor of melanin content in feathers of both sexes in Barn Swallows, with lower values (i.e. darker colors) denoting higher total eumelanin and pheomelanin content (McGraw et al. 2005). Although the white spots have a UV peak, the reflectance curves of prey and survivors overlapped in this range (see Fig. 1b), so that UV chroma (a measure of the contribution of UV to total reflectance) was not considered in addition to brightness. Brightness was defined as the

summed reflectance across the entire spectral range (300–700 nm; Montgomerie 2006).

Repeatability of color measurements was calculated following Lessells & Boag (1987). When both feathers were available in the case of prey, only one feather taken at random was used. Repeatability of brightness of the proximal and distal parts of feathers, when measured at different points, were low for both prey (proximal part: $r = 0.08$, $F_{29,61} = 1.27$, $p = 0.214$; distal part: $r = 0.11$, $F_{29,61} = 1.38$, $p = 0.146$) and survivors (1989: proximal part: $r = 0.46$, $F_{22,46} = 3.59$, $p < 0.001$; distal part: $r = -0.02$, $F_{22,46} = 0.93$, $p = 0.563$; 1993: proximal part: $r = 0.17$, $F_{38,78} = 1.60$, $p = 0.040$; distal part: $r = -0.07$, $F_{38,78} = 0.80$, $p = 0.779$). The values were considerably higher for the brightness of the white spot, which were measured at the same point (prey: $r = 0.67$, $F_{29,61} = 7.06$, $p < 0.0001$; survivors 1989: $r = 0.51$, $F_{22,46} = 4.19$, $p < 0.0001$; survivors 1993: $r = 0.60$, $F_{37,76} = 5.56$, $p < 0.0001$). This was expected if it is taken into account that the color of a tail feather changes along its length, so measures taken at different points of a single feather are necessarily variable. The aim of taking three color measures for each feather part was to collect information on heterogeneity of coloration. We also recorded measures for the proximal and distal parts of feathers repeatedly at a single point in order to calculate repeatability. Repeatabilities obtained this way were very high for both prey (proximal part: $r = 0.87$, $F_{29,61} = 203.76$, $p < 0.0001$; distal part: $r = 0.98$, $F_{29,61} = 209.83$, $p < 0.0001$) and survivors (1989: proximal part: $r = 0.93$, $F_{22,46} = 42.44$, $p < 0.0001$; distal part: $r = 0.99$, $F_{22,46} = 308.83$, $p < 0.0001$; 1993: proximal part: $r = 0.98$, $F_{38,78} = 129.29$, $p < 0.0001$; distal part: $r = 0.97$, $F_{38,78} = 100.26$, $p < 0.0001$). In order to use representative measures of heterogeneity of color, only measures taken at different points of feathers were introduced in the analyses.

We use the term “paler” instead of “brighter” throughout when referring to individuals with higher brightness of black coloration of tail feathers in order to avoid confusion with variability in conspicuousness. There is a traditional use in the literature of the term “bright” to refer to conspicuous individuals, but the functional use of brightness considered here has the opposite meaning because, at least for melanin-based plumage colors, it reflects the absence of pigment (McGraw et al. 2005). Thus, what has often been considered a bright black bird on the basis of human perception of color (e.g. Slagsvold et al. 1995) is actually (fol-

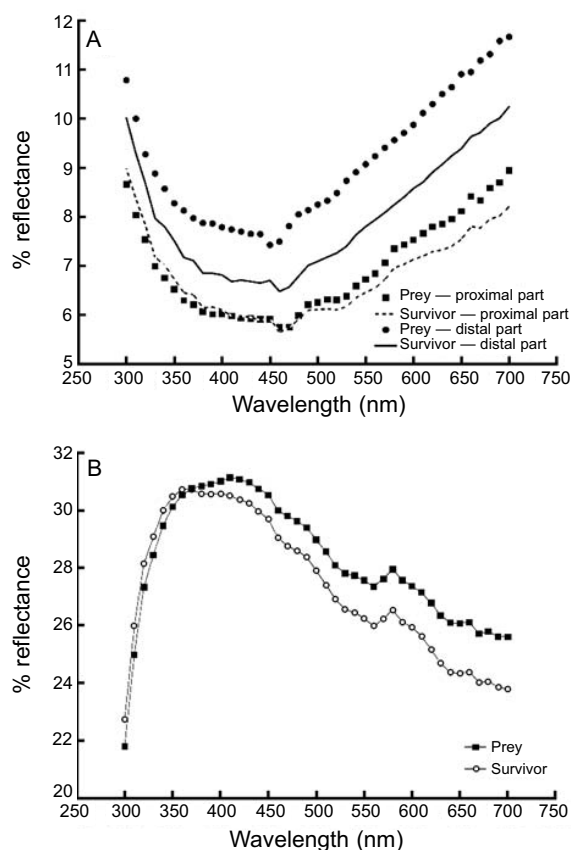


Fig. 1. Spectral reflectance of proximal and distal parts (a) and white spots (b) of outermost tail feathers in adult Barn Swallows that fell prey to Sparrowhawks or survived the breeding season. Error bars are omitted for clarity.

lowing our terminology) a dark bird. Therefore, we consider that Barn Swallows with darker tails are more conspicuous than those with paler tails rather than having lower values of brightness. Although objective measurements of conspicuousness need calculations of color contrast against the background as perceived by predators (Vorobyev et al. 1998), birds with darker tails being more conspicuous is what should be expected if melanin-based traits are indicators of individual quality (see Introduction). The Eurasian Sparrowhawk is a raptor that in the study area breed in small plantations and hunts predominantly by surprise in opens farmland, hedges or plantations (Cresswell 1994). In contrast, Barn Swallows are insectivorous aerial feeders that forage in open fields (Evans et al. 2007). Thus, the most likely encounters are those in which Sparrowhawks find swallows from forest patches and thus perceive them against the clear colors of the sky. It is therefore plausible that the darker the feathers, the more conspicuous the Barn Swallows.

Statistical analyses

We performed a MANOVA in which the three color measures taken on swallow tails (proximal part, distal part and white spot brightness) were introduced as dependent variables, and probability of survival (dead vs. alive), tail length and the interaction between these two terms were entered as fixed factors. The dependent variables were those describing the color of tail feathers instead of survival probability because we were interested in performing an exploratory analysis in order to search for possible differences in plumage color between prey and non-prey. Sex was introduced in previous analyses, but was removed from the final model because it did not significantly contribute to explain variance in any of the response variables (brightness of proximal part: $F_{1,86} = 2.66$, $p = 0.106$; brightness of distal part: $F_{1,86} = 0.02$, $p = 0.885$; brightness of white spot: $F_{1,86} = 0.82$, $p = 0.368$).

Because there were no significant differences between years in color variables (Student's t-test:

proximal part: $t_{60} = 0.28$, $p = 0.778$; distal part: $t_{60} = 0.37$, $p = 0.712$; white spot: $t_{59} = 0.59$, $p = 0.558$), or in the size of the white spot ($t_{60} = 0.68$, $p = 0.497$), all data were pooled. Visual inspections of residuals confirmed that normality assumptions were fulfilled.

RESULTS

In total, prey samples consisted of 23 male and 7 female Barn Swallows, while we obtained feathers from 32 male and 30 female survivors. The mean values of length and brightness of the outermost tail feathers for these groups are shown in Table 1.

Univariate analyses showed that there was an almost significant difference between prey and survivor Barn Swallows with respect to brightness of the distal part of the outermost tail feathers, prey having stronger reflectance values than survivors (Table 2, Fig. 2). This difference is considerably larger for birds with the longest tails, when individuals are separated into two groups with respect to median tail length (Fig. 2). The interaction between survival prospects of birds and tail length had a significant effect for the brightness of the distal part of feathers (Table 2). That was because the slope of the regression line between brightness and tail length was only significant and positive for Sparrowhawk prey ($t = 2.35$, $p = 0.021$, $\beta = 1.66$), but not for survivors ($t = 0.35$, $p = 0.724$, $\beta = -0.19$). Thus, the longer the tail the more bright the tail feathers, while no relationship was found for survivors (Fig. 3). In contrast, tail length was negatively correlated with the brightness of the proximal part of tail feathers ($r = -0.21$, $p = 0.044$; Table 2, Fig. 4), indicating that tails are darkened at their base as tail length increases. None of the factors contributed to explain variance in the brightness of the central white spot (Table 2).

The model explained a significant percentage of variance (9.2%; $F_{3,87} = 2.94$, $p = 0.038$) in brightness of the distal part of tail feathers only. The explained variance was lower for the proximal

Table 1. Mean values (\pm SE) of length (mm) of outermost tail feathers and brightness (summed reflectance) of the proximal and distal parts and the white spot of the feathers in prey and survivor male and female Barn Swallows.

	Tail length (mm)	Males			Tail length (mm)	Females		
		Proximal part	Brightness Distal part	White spot		Proximal part	Brightness Distal part	White spot
Prey	103.4 \pm 2.3	273.7 \pm 15.4	377.7 \pm 26.1	1154.0 \pm 32.7	86.6 \pm 1.5	324.3 \pm 23.2	360.5 \pm 29.9	1168.2 \pm 43.9
Survivor	107.8 \pm 1.5	262.4 \pm 11.1	334.6 \pm 19.5	1109.3 \pm 21.4	90.6 \pm 1.1	294.5 \pm 13.2	320.9 \pm 19.2	1130.5 \pm 21.1

Table 2. Results of multivariate analyses of variance (MANOVA) to investigate the effect of survival prospects of adult Barn Swallows (Sparrowhawk prey vs. survivors) and tail length on variance in brightness of the three parts considered to characterize the black (proximal and distal parts) and white color (central white spot) of the outermost tail feathers.

	Proximal part			Distal part			White spot		
	Wilks' λ	$F_{3,85}$	p	MS	$F_{1,87}$	p	MS	$F_{1,87}$	p
Survival prospects	0.96	1.22	0.307	300.6	0.06	0.803	39360.79	3.53	0.064
Tail length	0.91	2.72	0.049	20632.5	4.31	0.041	31530.13	2.82	0.096
Survival prospects @ Tail length	0.95	1.51	0.216	204.5	0.04	0.837	49275.04	4.41	0.038
Error	-	-	-	4789.0	-	-	11161.36	-	-

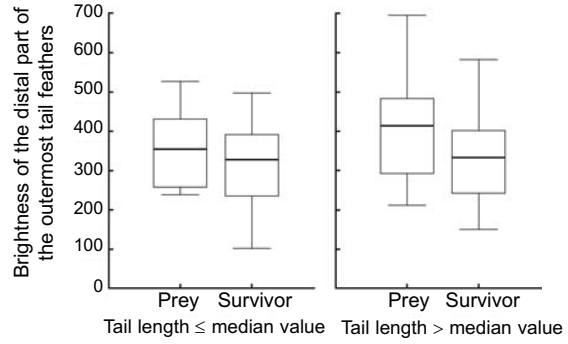


Fig. 2. Brightness of the distal part of the outermost tail feathers of prey and survivor adult Barn Swallows. Data are shown for two groups depending on whether tail length was below (left panel) or above (right panel) the median tail length (97.5 mm). Note that the difference in brightness between prey and survivors is more marked in the group with longer tails. The box-plots show median, inter-quartile range and non-outlier range.

part (5.1%; $F_{3,87} = 1.55$, $p = 0.207$) and the white spot (2.0%; $F_{3,87} = 0.60$, $p = 0.614$). Tail length was the only factor contributing to explain variance in the three color variables overall.

The area of the white spot of the outermost tail feathers did not differ between prey and survivors (Student's t -test: $t_{90} = 0.90$, $p = 0.370$), even when controlling for tail length (General Linear Model: survival prospects: $F_{1,88} = 1.12$, $p = 0.292$; tail length: $F_{1,88} = 19.84$, $p < 0.0001$; survival prospects \times tail length: $F_{1,88} = 0.91$, $p = 0.343$; model: $R^2 = 0.19$, $F_{3,88} = 6.99$, $p = 0.0003$).

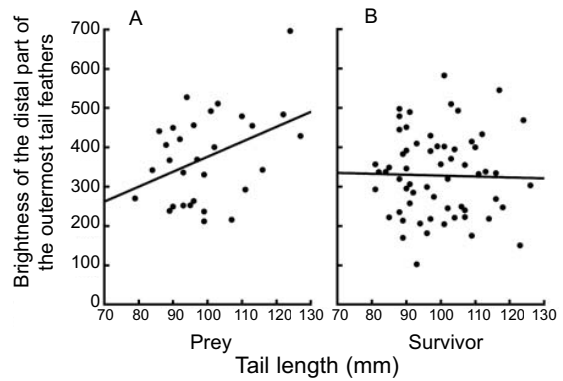


Fig. 3. Relationship between the brightness of the distal part of the outermost tail feathers and tail length in prey and survivors of adult Barn Swallows. The point with the largest brightness value in A) is not an outlier as indicated by a Cook's distance lower than 2 (0.59; Crawley 1993), and the tendency remained when this point was removed from the analysis ($r = 0.25$, $p = 0.186$). The lines are the linear regression lines.

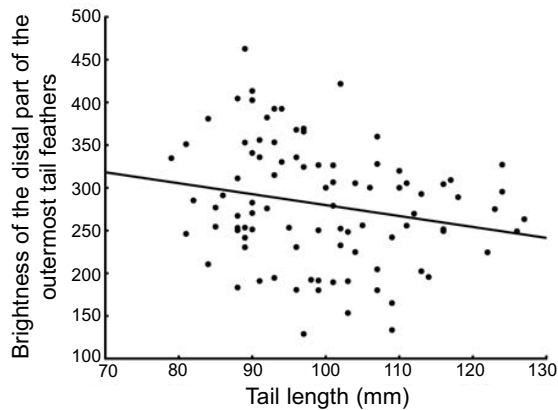


Fig. 4. Relationship between the brightness of the proximal part of the outermost tail feathers and tail length in adult Barn Swallows. The line is the linear regression line.

DISCUSSION

Signal theory (Zahavi 1975, 1977, Hasson 1997) suggests that only individuals of higher genotypic or phenotypic quality are able to overcome the costs of elaborate secondary sexual traits, thus showing a positive relationship between viability and ornamentation, as is generally the case in studies of ornamentation and viability (Jennions et al. 2001). An intrinsic prediction from this theory is that the predation cost of bearing exaggerated secondary sexual traits is larger for low quality individuals, contrary to predictions from sexual selection theory (Baker & Housome 1983). Therefore, according to the unprofitable prey hypothesis, natural selection promotes rather than constrains the evolution of conspicuous traits that evolve due to sexual or social selection (i.e. when they are honest indicators of individual quality and viability; Baker & Housome 1983, Götmark 1992, 1993, 1995, Caro 1995, Penteriani et al. 2008). Alternatively, they may specifically evolve to warn predators of the bearer's quality (pursuit-deterrence and aposematic signals; Caro 1995). Thus, predators could use such signals to increase the probability of successful prey capture by choosing signal characteristics that reflect weakness. Such a mechanism could be mediated by a learning process, or by differences in conspicuousness helping the predator to distinguish between individuals differing in quality (Sherratt & Beatty 2003, Penteriani et al. 2008). Alternatively, predators could indirectly select against trait components that reflect low quality just because the probability of capturing a low quality individual is

higher. The present study supports this hypothesis rather than the classical assumption of sexual selection theory that more colorful individuals pay a cost in terms of predation (Slagsvold et al. 1995, Dale & Slagsvold 1996), perhaps because this latter prediction only functions at an interspecific level (Götmark 1993, Slagsvold et al. 1995, Dale & Slagsvold 1996, Rytönen et al. 1998, Møller & Nielsen 2006).

Direct effects of predation on secondary sexual traits have only rarely been documented. Møller & Nielsen (1997) showed that Barn Swallows falling prey to Sparrowhawks had shorter and more asymmetrical tails than survivors. In this species, males with longer and more symmetrical tails have both higher mating success and viability (Møller 1994, Saino et al. 1997). Here, using the same samples as Møller & Nielsen (1997), we have found that color of the tail of Barn Swallows is another trait on which predation independently acts differentially. As predicted, swallows that became prey had paler tails than survivors, but this effect was due to a positive relationship between tail brightness and tail length that was not found in survivors. This finding indicates that birds with long tails that are not able to melanize their feathers at a level expected for a given tail length are easier captured by Sparrowhawks, suggesting that tail elongation in Barn Swallows may be constrained by the capacity of depositing melanin in tail feathers.

Recently, Galván & Alonso-Alvarez (2008, 2009) have shown that eumelanin-based traits are costly to produce because eumelanogenesis requires low levels of a key intracellular antioxidant (i.e. glutathione), thus limiting the capacity of expressing these traits to those individuals of high enough quality to compensate the low levels of glutathione with the production of alternative antioxidants. Furthermore, the production of melanin-based traits seems to be environmentally constrained because it can depend on the availability of food resources, which enforces signaling of phenotypic quality (Anderson et al. 2002, Poston et al. 2005, Fargallo et al. 2007, Galván et al. 2010). The results of the present study lend support to these ideas, as paler individuals, which are those with lower melanin contents (McGraw et al. 2005), were preferentially captured by Sparrowhawks. As these birds that became prey also had shorter and more asymmetrical tails than survivors (Møller & Nielsen 1997), melanin-based color of their tails seems to be another indicator of quality in addition to tail length and symmetry

(Møller 1994), demonstrating the complexity of this ornament.

The positive correlation found between tail brightness and tail length only in birds that fell prey to Sparrowhawks suggests a novel cost of producing long tails in Barn Swallows. Because these two attributes are indicators of individual quality (see above), a trade-off between producing a long tail and a dark tail is possible. Indeed, the difference in brightness between prey and survivors was larger among birds with the longest tails. Such a trade-off is likely to exist, because melanin increases the stiffness and resistance of feathers to abrasion (McGraw 2006, Schreiber et al. 2006). In fact, the structural integrity (high density of barbules) of melanic feathers is negatively and positively related, respectively, to the size and darkness of the melanic plumage patch in other bird species (Galván 2011). This suggests that a compromise exists between producing melanic plumage traits that are both large and have a high structural integrity and that melanization increases the structural integrity of feathers (Galván 2011), and it is likely that integrity determines the performance capacity of feathers. If the outermost tail feathers provide aerodynamic benefits to Barn Swallows (Norberg 1994), and mechanical fatigue decreases the stiffness of feathers (Borguud 2003), it is reasonable to assume that melanin deposition in feathers should be proportional to the mechanical strain on feathers. Thus, a long tail that is not appropriately darkened through melanin deposition would not confer the aerodynamics benefits of long outermost tail feathers achieved by individuals that are able to do so, thereby increasing the risk of being captured by predators. Therefore, differential predation by Sparrowhawks reported here may be a consequence of low quality individuals being easier to catch, rather than being mediated by active learning or recognition by Sparrowhawks of the profitability of prey (Sherratt & Beatty 2003, Penteriani et al. 2008). This implies that conspicuousness is unlikely to play an important role by mediating differential predation, as expected if it is taken into account than differences in brightness between prey and survivors are small (Fig. 1a).

On the other hand, the negative relationship between tail length and brightness of the proximal part of the tail found for all Barn Swallows supports the assumption that melanin deposition is proportional to feather length. The fact that no relationship between tail length and brightness was found in the distal part of the tail of survivors

suggests that the color of the distal part could act as a revealing handicap. Barn Swallows may thus maximize the ratio of length to brightness because the length of the distal part plays a role in sexual selection (Møller 1994), or because tail length is more important than brightness in sexual selection. Predation could act on tail length relative to color of tail feathers because individuals with long, but pale tail feathers would be less able to escape predation due to the small amount of melanin deposited in their feathers. Therefore, the quality-revealing signal may not be tail color per se, but rather the ratio of tail length to tail brightness.

Although Perrier et al. (2002) found no evidence of dorsal iridescent black coloration of Barn Swallows being a sexually selected trait, it is noteworthy that in the present study differences in brightness between prey and non-prey were only found at the distal part of the outermost tail feathers but not at the proximal part. This finding differs from the color patch studied by Perrier et al. (2002) because tails do not have a clear UV peak (see Fig. 1a), and they are not clearly iridescent. Because the proximal part is covered by adjacent tail feathers and the tail coverts, when the tail is folded, only the distal part is visible. Thus, the distal part can be assessed by female Barn Swallows when males display their tails to attract potential mates (Møller 1994). Because we have found that melanin-based coloration of tail feathers is an indicator of individual quality, it has the potential to be under sexual selection, something that should be investigated by future studies.

Finally, we found no difference in the brightness of the white spot of tail feathers between prey and non-prey. Hanssen et al. (2006) and McGlothlin et al. (2007) have suggested that the degree of plumage whiteness is an indicator of individual quality in female Common Eiders *Somateria mollissima* and in male Dark-eyed Juncos *Junco hyemalis*, respectively. Thus, only the size of this patch seems to act as a quality-revealing signal in Barn Swallows (Kose & Møller 1999, Kose et al. 1999), while the actual coloration of this spot seems less important, as shown by the present study. Differences between prey and survivors were not found either in the size of the white spot, reinforcing the idea that differences in the intensity of melanin-based color between these two groups of birds may be due to the mechanical properties conferred by melanin to feathers. This also suggests that the production of melanin-

based and white (i.e. unmelanized) traits may be controlled by different mechanisms.

In conclusion, we compared the coloration of the outermost tail feathers of adult Barn Swallows of prey captured by Sparrowhawks and survivors, showing that the dark coloration of the distal, but not the proximal part of tails predicted predation risk. This finding is consistent with the hypothesis that tail coloration acts as a revealing handicap, with predators mainly capturing individuals that had pale feathers relative to the length of feathers.

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STRESZCZENIE

[Presja drapieżnicza a ubarwienie upierzenia opartego o melaninę u dymówki]

W pracy testowano hipotezę, że drapieżnictwo krogulca na dymówkach związane jest kolorem ich sterówek (odpowiadają za niego głównie barwniki melaninowe), który może być, wyznacznikiem jakości osobnika. Zbierano pióra dymówek, które padły ofiarą krogulca, oraz od żywych ptaków z pobliskiej kolonii lęgowej. Mierzono długość oraz, na podstawie spektrofotometrii, kolor najbardziej zewnętrznych sterówek (Fig. 1). Kolor piór analizowano dla trzech części — wewnętrznej (bliższej dutki), zewnętrznej, oraz przedzielającej je białej plamy (Tab. 1). Pióra, które na podstawie pomiarów spektrofotometrycznych standardowo uznaje się za bardziej jaskrawe, zawierały mniej barwników melaninowych, i w tym znaczeniu określane były w pracy jako bledsze.

Stwierdzono, że osobniki, które padły ofiarą krogulca miały bledszą część zewnętrzną sterówek, przy czym różnica ta była silniej zaznaczona w grupie ptaków o długości ogona powyżej mediany (Fig. 2). Nie było natomiast różnic w jaskrawości ubarwienia dla części bliżej dutki, ani dla białych plam (Tab. 1, 2). W grupie ptaków, które padły ofiarą krogulca, istniała dodatnia zależność pomiędzy jaskrawością części zewnętrznej sterówki i długością ogona — ptaki z dłuższymi ogonami miały bledszą część zewnętrzną sterówek. Natomiast w drugiej grupie ptaków oba parametry nie były ze sobą powiązane (Fig. 3). Ponadto, jaskrawość części wewnętrznej sterówek była ujemnie skorelowana z długością ogona (Fig. 4).

Wyniki pracy wskazują, że u dymówki szczególnie osobniki z długim ogonem (cecha preferowana przez samice w doborze płciowym), które nie są w stanie odłożyć w tych piórach odpowiednio dużo melaniny, ponoszą koszty zwiększonego prawdopodobieństwa schwymania przez drapieżnika.